Reference: *Biol. Bull.* **183:** 94–98. (August, 1992)

Tolerance of Infaunal Benthic Foraminifera for Low and High Oxygen Concentrations

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Abstract. *Ammonia beccarii* is irregularly distributed in the subtidal sediment of the southern North Sea, with substantial numbers occurring as deep as 35 cm below the water-sediment interface. Deep infaunal specimens are insensitive to high oxygen concentrations (±225 μM), and all specimens isolated from different depth intervals continued their normal activities (feeding and growth) when exposed to dysaerobic oxygen content (<12.5 μM). Specimens of *E. excavatum*, *Q. seminulum*, and *E. scabra*, when subjected to the same conditions, behave similarly to *A. beccarii*. These benthic foraminifera have very low oxygen requirements.

The chambers of *A. beccarii* that are formed *in situ* at different depth intervals in the sediment have a wide range in the porosity (*i.e.*, % of area occupied by pores) which is adequate for gas exchange under both high and low oxygen conditions. However, chambers formed in the laboratory under dysaerobic conditions have a significantly higher porosity (mainly due to larger pores) than do chambers constructed in well oxygenated water.

Foraminifera live at the oxic-anoxic boundary throughout the sediment and therefore must occasionally be subjected to completely anoxic conditions. *A. beccarii*, *E. excavatum*, and *Q. seminulum* actively survived at least 24 h without oxygen, indicating that they are capable of facultative anaerobic metabolism.

Introduction

Benthic foraminifera occur epiphytically, epizoically, epifaunally, and infaunally (*e.g.*, Buzas, 1974; Thiel, 1975; Coull *et al.*, 1977; Alexander and DeLaca, 1987; Bernhard, 1989; Lutze and Thiel, 1989). They evidently exploit all benthic marine environments, and some soft-shelled forms also inhabit empty foraminiferal tests (Gooday, 1986; Moodley, 1990a).

There seem to be two general trends in the vertical distribution of benthic foraminifera in soft sediments. In deep-sea environments, certain species have their maximum densities in deeper sediment layers (below the upper two centimeters) and appear to prefer the associated low oxygen concentrations (Corliss, 1985; Mackensen and Douglas, 1989). The advantage of active migration to these deeper layers would be less competition and predation (Gooday, 1986; Mackensen and Douglas, 1989). There is some evidence that infaunal species are adapted to their habitats, having greater pore densities evenly distributed over most of the test (in response to low oxygen content); their tests have rounded edges and planispiral coiling or have ovate or cylindrical shapes. In contrast, epifaunal species (that live on and within the upper centimeter; Corliss, 1985) are biconvex or plano-convex and either lack pores or have large surface pores on only one side of the test (Corliss and Emerson, 1990).

In shallow subtidal and intertidal areas, the vertical distribution of benthic foraminifera is irregular without a consistent stratification of species. The occurrence of Foraminifera in deeper layers has been attributed to passive transport resulting from bioturbation (*e.g.*, Collison, 1980; Langer *et al.*, 1989), and substantial numbers are often encountered below the oxygenated layer (Bernhard, 1989; Moodley, 1990b). When food is abundant throughout the sediment, there seems to be no need for foraminifera to concentrate at any particular level or for species to partition their habitat vertically (Thiel, 1983). Further, the extent to which they can maintain a desired depth depends on the physical (water movement) and biological (macrofaunal activities) stability of the sediment.

The availability of food determines the maximum habitat depth in deep-sea sediment, which varies from 6 to 15 cm (Coull *et al.*, 1977; Corliss, 1985). Oxygen avail-

Received 2 October 1991; accepted 18 May 1992.

ability may set the limits in shallow areas, which generally have a larger supply of organic matter (Gooday, 1986): Foraminifera have been reported to be living at core depths of 30–35 cm in such areas (Goldstein, 1988; Moodley, 1990b). Although Foraminifera sampled from below the oxic layer have been reported to be alive (as assessed by cytoplasmic stainability or cytoplasmic streaming), actual activity under dysaerobic or anoxic conditions has not been demonstrated.

In a shallow, organically enriched zone in the southern North Sea, oxygen penetration in May 1990, excluding the local subduction by macrofauna, was only 4.5 mm, yet the majority of the foraminiferan population was encountered below this depth. The differences in infaunal densities of foraminifera in this area have been related to the type of bioturbation (Moodley, 1990b). *Ammonia beccarii* (Linné), like all other foraminifera, had maximum numbers within the upper 5 cm, but remained common down to 35 cm (Moodley, 1990b).

Deep infaunal specimens are exposed to low oxygen concentrations. Therefore, to test whether infaunal and epifaunal specimens of *A. beccarii* differ in their sensitivity to different oxygen concentrations, specimens were isolated from different depth intervals and exposed to both high and low oxygen concentrations. Some species, like *A. beccarii*, have pores both on the dorsal and ventral side. To search for further variation in the response to low oxygen concentrations, pores in *A. beccarii* were counted and pore diameters measured, for chambers constructed under different conditions. Specimens of *Elphidium excavatum* (Terquem), *Quinqueloculina seminulum* (Linné) and *Eggerella scabra* (Williamson) were also exposed to the same conditions but were not examined in detail.

Because they occur at the oxic-anoxic boundary throughout the sediment, a few species of foraminiferans were maintained totally without oxygen, and their fate under these conditions was determined. *A. beccarii* was examined for methanogenic bacteria because anaerobic protozoans sometimes certain symbiotic methanogenic bacteria that take up the protons formed when the protozoans remove reduction equivalents as hydrogen (Van Bruggen *et al.*, 1983; Fenchel, 1987).

Material and Methods

Sediment samples were collected several times during 1989 and 1990 with a Reineck box-corer from the Frisian Front area in the southern North Sea (Moodley, 1990b). This area (40 m water depth) is characterized by a fine grained sediment with a high POC content (1.29% in June and 0.55% in February; Moodley, 1990b). Subsamples were taken from the box-cores with a PVC pipe (O 9.5 cm). On boards centimeter slices of the cores were immediately made; the slices were kept in glass jars with seawater and maintained at ambient temperature until the initiation of the experiments. The following intervals were sampled: 0–1, 4–5, 9–10, 14–15, 19–20, 29–30, and 34–35 cm.

Benthic foraminifera occurring in soft sediments feed by first concentrating particles around the aperture or test, forming a food cyst; the presence of empty cysts, or of particles attached to the tests, would indicate that the protozoans were active under the maintenance conditions. In polythalamous (multi-chambered) species, growth is achieved by the construction of a new chamber, and an increase in the number of chambers is also used as an indicator of activity under the different conditions. Just before the beginning of every experiment, each foraminiferan specimen was cleaned under the dissecting microscope (all attached particles were removed from the test with a brush). The maximum diameter of the test was then measured and the number of chambers counted under the inverted microscope. Every foraminiferan used in the experiments was isolated from field samples that had been collected no more than three days before the start of the experiments.

The sensitivity of *A. beccarii* to high oxygen levels was examined as follows. Specimens of the same size range were isolated from different depth intervals (n = 21, 1–5 specimens per depth interval) and maintained with fresh detritus as food, at 15°C and without light, until they built a new chamber. The detritus was either the <50 μm fraction removed from surface sediment or heat-killed *Chlorella*. These benthic foraminifera, maintained only with detritus as a food source, have been observed to grow and reproduce in the laboratory (Moodley, unpub.). High oxygen concentrations (±225 μM, monitored with an oxygen meter) were maintained by frequently replacing the seawater with well oxygenated seawater. Specimens of *E. excavatum* (n = 3), *E. scabra* (n = 4), and *Q. seminulum* (n = 4) were also included in this experiment.

To examine their behavior under low oxygen conditions, another set of foraminiferans isolated from different depth intervals (n = 12, 1–2 specimens per depth interval) were maintained with less than 12 μM O_2. The low oxygen content was obtained by extensively flushing the seawater in the maintenance vessel with nitrogen (N_2 type 6.0, that was guaranteed to contain <12.5 μM O_2, Air Products, Nederland BV) until the reading on the oxygen meter passed the zero value. Zero calibration was done with a zero-oxygen solution (HI 7040, Hanna Instruments USA). The maintenance vessel, constructed especially for these experiments, was hermetically sealed and kept for 6 days without any increase in oxygen content, as registered by constant monitoring. Specimens of *E. excavatum* (n = 6), *E. scabra* (n = 7), and *Q. seminulum* (n = 4) were also exposed to low oxygen concentrations.

Table I

Sensitivity of specimens from [illegible] intervals (cm) in the sediment to different [illegible] concentrations

Depth interval	High ox (±225 μ				Low oxygen (<12 μM)				Anoxic[a]			
	A	Eg	[illegible]	Q	A	Eg	El	Q	A	Eg	El	Q
0–1	++	+	nd	nd	++	+	nd	nd	+	nd	+	+
4–5	++	+	+	nd	++	nd	+	nd				
9–10	+	nd	++	nd	++	+	+	nd				
14–15	++	nd	nd	nd	+	+	+	nd				
19–20	++	nd	nd	+	++	nd	nd	+				
29–30	++	+	+	nd	++	+	+	nd				
34–35	++	nd	nd	nd	++	+	+	nd				

[a] For the anoxic experiment, only specimens isolated from upper cm of the sediment were used (n = 8). The number of specimens of each species from different depth intervals exposed to high or low oxygen varied from 1 to 5 specimens. A = *A. beccarii*, El = *E. excavatum*, Eg = *E. scabra*, Q = *Q. seminulum*. (+) = active, (++) = active and growing, nd = no data.

Morphological variation in *A. beccarii* in response to different oxygen concentrations was also examined. The pore characteristics of the chambers constructed under maintenance conditions were measured. Individuals maintained under high oxygen and individuals maintained under low oxygen were compared.

Specimens were isolated from different depths in the sediment, and the pore characteristics of the tests were evaluated. Because a few specimens had aberrant last chambers, the penultimate chamber was used for this analysis of *in situ* test formation at different depths.

The pores on the dorsal side of the chambers (visualized on SEM micrographs) were counted and a standard area calculated. The pore diameters were also measured and considered together with pore density as porosity (*i.e.*, % of chamber area occupied by pores), as calculated by Frerichs *et al.* (1972). The significance of the differences were tested with the Mann-Whitney *U* Test.

In the third experiment, specimens of *A. beccarii* (n = 1), *E. excavatum* (n = 2) and *Q. seminulum* (n = 5), isolated from surficial sediment, were exposed to anoxic conditions for 24 h with detritus as food. The maintenance vessel was kept at room temperature (±20°C) without light. Anoxic conditions were obtained by first extensively flushing with nitrogen and then removing traces of oxygen with ascorbic acid (a strong reducing agent; 0.13%), and then immediately hermetically sealing off the vessel. The above treatment also results in a color change of resazurin and methylene blue; these redox indicators were individually added to control vessels lacking foraminifera, verifying the reduced conditions of the maintenance medium which was buffered with 30 mM sodium bicarbonate.

Methanogenic bacteria are characterized by fluorescent coenzymes that are easily detected by epifluorescence microscopy (Van Bruggen *et al.*, 1983; Fenchel, 1987), so this method was used to search for symbiotic methanogenic bacteria in *A. beccarii*.

Results

Deep infaunal specimens proved to be insensitive to high oxygen concentration, for they continued feeding and growing (Table I). All of the specimens examined continued to be active even at extremely low oxygen concentrations (<12 μM). Activity was not restricted to feeding; six specimens of *A. beccarii* also continued growing at low oxygen levels (Table I).

There is a wide range in the porosity of chambers of *A. beccarii* constructed *in situ* at different depth intervals in the sediment (Fig. 1). But the porosity of the chambers constructed in the laboratory under dysaerobic conditions is significantly higher than that of the chambers formed under well oxygenated conditions (±225 μM; Table II). This difference is mainly due to a significant difference in pore diameter, and not in pore density (Table II).

All specimens actively endured 24 h without oxygen (Table I), as implied by the presence of particles around the test or aperture. In one of the trial experiments (not included in Table I) inadequate buffering resulted in a drop in pH (to <6) causing the almost total decalcification of the foraminifera; nevertheless they were still alive and active under anoxic conditions.

No methanogenic bacteria were detected in *A. beccarii*. This is not strange since methanogens are considered to be extremely sensitive to oxygen.

Discussion

With an oxygenated layer only a few millimeters thick, infaunal specimens are totally dependent on the burrow-

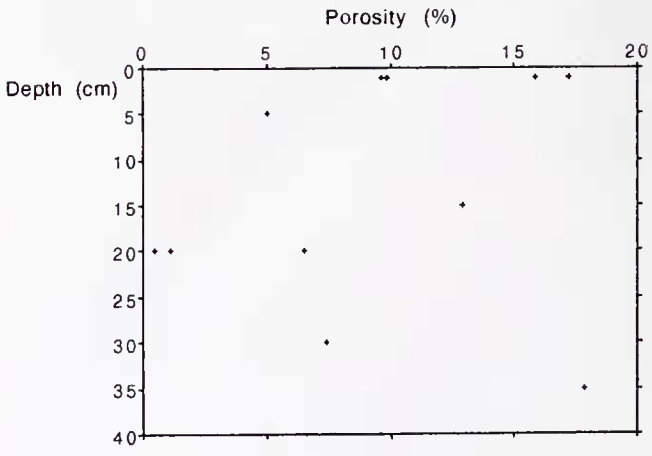

Figure 1. Porosity of the penultimate chambers of *Ammonia beccarii* formed *in situ* at different depth intervals in the sediment.

Table II

Comparison of pore characteristics in chambers of Ammonia beccarii *formed under different oxygen concentrations*

	Pore density		Pore diameter		Porosity	
	H	L	H	L	H	L
	1284	559	1	1.8	10.1	14.2
	1083	410	1.13	1.6	10.9	8.2
	715	653	1.08	2	6.5	20.5
	1391	84	0.8	0.7	7	0.3
	1001	221	1.08	2.37	9.2	9.7
	235	842	1.08	1.76	2.2	20.5
	144	780	0.3	1.35	0.1	11.2
	841	905	0.67	1.35	3	12.9
	671		0.7		2.6	
Mean	815	557	0.87	1.62	5.73	12.19
SD	430	297	0.28	0.5	3.9	6.62
Statistical difference	ns		$P > 0.005$***		$0.025 > P > 0.01$**	

Pore densities (#/10^4 μm^2), pore diameters (μm) and porosity (%) of the chambers formed in maintenance under high (± 225 μM = H) and low (<12.5 μM = L) oxygen concentrations with statistical differences (Mann-Whitney U Test).

ing activities and irrigation of macrofauna for their oxygen supply. Depending on the type of bioturbation, foraminifera are transported to deeper layers and, at the same time, are provided with food and oxygen or are simply buried and then subjected to anoxic conditions. They generally exhibit negative geotaxis (Richter, 1964; Lee *et al.*, 1969; Severin and Erskian, 1981; Moodley, 1990b), and this behavior ensures, to a certain extent, their position in more favorable layers with respect to food and oxygen availability. When the supply of oxygen is cut off, *e.g.*, because the burrower has moved, they are subjected to anoxia that they can endure for at least 24 h. The presence of particles around the test or aperture indicates pseudopodial activity under anoxic and dysaerobic conditions, so they are capable of migrating to more favorable layers, permitting aerobic metabolism with a higher ATP-yield. Bolivinids and buliminids burrow into oxygen-depleted layers (Kitazato, 1981) and may be able to endure anoxic conditions for even longer periods.

Facultative anaerobiosis is not uncommon in free-living Protozoa (Fenchel, 1987; Anderson, 1988) and in marine infaunal invertebrates: *e.g.*, various bivalve mollusks (see Zwaan, 1977), polychaete worms *Arenicola marina* (see Zebe, 1975), and *Nereis diversicolor* (see Schöttler, 1978). In all cases, some sort of fermentation process provides metabolic energy. Considering the environment these benthic foraminifera inhabit and their very slow movement (0.84–30.0 mm/h; Kitazato, 1988), facultative anaerobiosis would seem to be necessary for their survival. Although no symbiotic methanogenic bacteria were found in *A. beccarii* from the southern North Sea with well-oxygenated bottom water, foraminifera living in sediment below anoxic waters (*i.e.*, exposed to prolonged anoxic conditions) may very well have symbionts, as earlier suggested by Kitazato (1989) for infaunal species. However, under constant, totally anoxic conditions benthic foraminifera are absent (Murray, 1991).

A wide range in porosity in *A. beccarii* (Fig. 1) is apparently adequate for gas exchange under both low and high oxygen conditions (Table I). But gas exchange is increased when pores are larger (Table II). Indeed, foraminiferan gas exchange is enhanced by the concentration of their mitochondria under pore openings (Leutenegger and Hansen, 1979), which would be maximized by larger pores. Hofker (1968) noted that the pore diameter of Cretaceous gavelinellid species increases progressively with test volume and attributed this phenomenon to greater respiratory requirements. However, the function of pores in gas exchange does not exclude other functions (Leutenegger and Hansen, 1979).

Benthic foraminifera evidently have very low oxygen requirements and respiration rates (Bradshaw, 1961; Lee and Muller, 1973). They belong to the subphylum Sarcodina that, as a group, also seems to have lower metabolic rates when compared to flagellates and ciliates of the same size (Fenchel, 1987). Benthic foraminifera have also been reported to grow and reproduce slightly below the oxidized zone (Matera and Lee, 1972). That low oxygen concentration is not a limiting factor for their existence is also corroborated by field observations. For example, as a result of a depressed oxygen level (0.21 ml l^{-1} or 9.24 μM O_2) in the winter of 1979-80 in the deep basin (115 m) of the Gullmar Fjord, Sweden, the macrofaunal component of the fauna disappeared. In contrast, the meiofauna exhibited no clear signs of being affected and, of all the meiofaunal taxa, the foraminifera seemed to withstand these conditions best (Josefson and Widbom, 1988). Deep-sea benthic environments with *continuous* dysaerobic conditions (oxygen-depleted bottom waters) support large standing stocks, but a low diversity of benthic foraminifera (*e.g.*, Phleger and Soutar, 1973; Douglas *et al.*, 1980; see Mackensen and Douglas, 1989). This could probably be explained in terms of different tolerance levels of oxygen concentrations for survival and reproduction. Additionally, assemblages that predominate during prolonged or continuous dysaerobic conditions consist mainly of flattened (shapes with a high surface area/volume ratio), unornamented, highly perforate, and thin walled forms (Bernhard, 1986).

Acknowledgments

We thank J. E. van Hinte and G. C. Cadée for their critical review and valuable suggestions. R. P. M. Bak and

J. H. Vosjan are gratefully acknowledged for their comments. Many thanks to E. Epping and C. G. N. de Vooys for essential discussions on the subject of anaerobic culture. The paper benefited from criticism by two anonymous reviewers. All maintenance vessels were constructed by the technical staff of the NIOZ (The Netherlands Institute for Sea Research).

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